Responses to referee comments

egusphere-2025-2180

BORIS-2 – a benthic ecosystem model based on allometry

Martin et al.

We thank both referees for their constructive comments and respond to each of them in turn.

All line numbers refer to lines in the version with tracked changes.

User manual supplement and Zenodo code have both been updated to match revised manuscript and a new Zenodo doi created and used throughout.

Referee 1

The manuscript describes the BORIS-2 model, a benthic ecosystem model based on class size that builds on a previous version that simulated ecosystems with a smaller size range and different representation of physiological processes. It describes a steady state solution used to test and evaluate the model and compare it to data from five different sites with a range of depths and overlying pelagic environments.

The authors did an excellent job organizing the manuscript; the explanation on the model itself, the validation and choice of coefficients, and the differences between the current version and BORIS-1 are well written and well linked when necessary. The arguments justifying the choices that need to be made to choose general coefficients and forcings to represent the different sites are well argued and informative for users that may want to run a transient version.

The figures and tables are clear and contain all the necessary information.

We thank the referee for their comments

In my view the paper is suitable for publication, although I do have a few of suggestions on the text:

Line 289-291: It seems reasonable to me to use the sediment traps at 3000 m, but out of curiosity, how much to they diverge? Thinking of future exercises linking ecosystem to sediment diagenetic processes, information of resuspension/sedimentation is always useful

This is a good question. We should have been more specific. At PAP (the only one of our study sites with a sediment trap time series) the flux near-bottom is often found to be in excess of that at 3000m because of re-suspension. Using the deep trap data therefore risks counting the same POC arriving on the seafloor twice. We have now added this information and supporting references to the text - lines 331-333.

Line 304-307: these sentences could be linked better

Agreed. We have tried to make this point more clearly. Lines 350-356

Line 519-521: The global estimate of carbon burial also shows spatial variation, thought to be much higher in shelf environments. I would assume there could be differences between the shallower and deeper sites chosen for model validation that could be mentioned or briefly discussed here.

An excellent point that we had missed, thank you. We have modified the text to clarify that the fraction buried does vary with water depth and that our decision to leave it out of the model is based on the deep-sea values. We have also given an indication of how this geographical variation could be added in future if needed. Lines 643-647

Referee 2

In this manuscript Martin et al. provide a model description and evaluation of an updated benthic community model, BORIS2. This model is a size based model of benthic heterotrophs / detritivores and extends the size range of the previous BORIS model both on the lower and upper ranges. Compared with the previous BORIS model, this second version also makes a number of improvements on the assumptions around metabolism and ingestion. This model is evaluated against 5 sites, including abyssal sites at the Porcupine abyssal plain and clarion clipperton zone. The inclusion of these two deep sites makes it so that this model is much more readily applicable for regional or other large-scale domains.

We thank the referee for their assessment and for their very helpful, specific recommendations which follow. Anieke Brombacher has contributed a lot of extra work in the additional modelling required to respond to these and so she has been moved to second author to reflect this increased contribution. This is also reflected in a revised "Author contribution".

Further testing arising from the referee's comments have directly led to a few modifications to parameter values that are worth noting now, as they inform several subsequent responses:

- Further study revealed that the previous set of parameter values led to proportionally greater energy use by larger organisms. Observations and theory indicate that an even distribution across sizes (referred to as energy equivalence) may be more typical. The scaling of the metabolic and interference parameters (α) has been adjusted to achieve this; by changing the rate scaling from -0.1 to -0.2 and the interference scaling (β) from -0.26 to -0.2. It is necessary to have $\alpha=\beta$ for energy equivalence. This required adjustment of the pre-factors for growth, respiration and mortality to continue to meet the constraints already described in the paper. The upper limit for respiration rate of bacteria was also increased to facilitate this based on a higher value found in the literature which is cited. Section 2.5 has been revised and expanded to describe this fully.
- It was realised that even though there is very large uncertainty in the observed TOC values, they can be used more objectively to constrain the interference pre-factor. This is now described in the manuscript (lines 531-536). The parameter value has been increased from 500 to 2000.

Modification of the parameter values means that Figures 3, 4, 6 and 7 (previously 2,3,4 and 5) and Tables 1 and 2 have all been revised using the new parameter values.

Main comments

My primary concern in this manuscript surrounds the introduction of the interference parameter, a_i. This parameter is described as the competitive interference between other scavengers, and shows up in the growth/feeding equation as modifying the biomass B. My concern about this primarily is because the size scaling parameters for the other processes are all identical (see next paragraph) – the entirety of the emergent structure of the community relies on this single parameter, which is very poorly understood and is not common to other ecosystem models. The functional form of the feeding relationship changes such that if you were to rewrite it to an equivalent Monod-like relationship, it would be g*f(R,B) = gR/(R+aB) but instead of a fixed half-saturation constant, aB varies with mass. So then the initial slope becomes R/aB. While I am not doubting that the introduction of a

size-dependent scaling for Biomass in this feeding relationship could be useful, unfortunately I am also not convinced of the need for it either. Perhaps it is because I am not familiar with DeAngelis et al. 1975. To convince readers, perhaps the authors could show plots of this functional form (at a minimum), and ideally some more plots showing the authors' central claim here, that you cannot achieve an emergent community structure in this model that matches observations without this parameter included.

The influence of the interference parameterisation goes further than the quality of the fit to observations. It is required to ensure that the model is not 'degenerate' i.e. can have multiple different solutions for the same parameter values. In this aspect it performs a similar structural role to a predation closure, suggested by the referee and discussed below.

We provide two pieces of evidence to show that removing the interference parameterisation leads to a degenerate model. First, take the current equation for how biomass of organisms in each size class varies with time and remove the influence of interference by replacing $f=R/(a_iB_i+R)$ with $f_{noint}=R/(k+R)$ where k is a constant:

$$\frac{dB_i}{dt} = \overbrace{g_i \cdot f_{noint} \cdot B_i}^{gross\ growth} - \overbrace{r_i \, . B_i}^{respiration} - \overbrace{m_i \, . B_i}^{mortality}$$

At steady state, this gives us $g_i \, . f_{noint} - r_i - m_i = 0$ which gives an equation for R but provides no constraint on B_i. The new equation for rate of change of detritus

$$\frac{dR}{dt} = F - \sum_{i=1}^{N} \left[\overbrace{g_i \cdot f_{noint} \cdot B_i}^{gross\ growth} - \overbrace{m_i \, . B_i}^{mortality} \right]$$

involves a sum over the contribution of all size classes, so does not provide a constraint for the biomass of an individual size class. A larger biomass of one size class can be balanced by a smaller one for another. This means that different initial conditions for B_i can lead to different solutions. The second piece of evidence is shown in Figure R1, demonstrating that running the model with f replaced with f_{noint} for different initial conditions does indeed lead to different solutions.

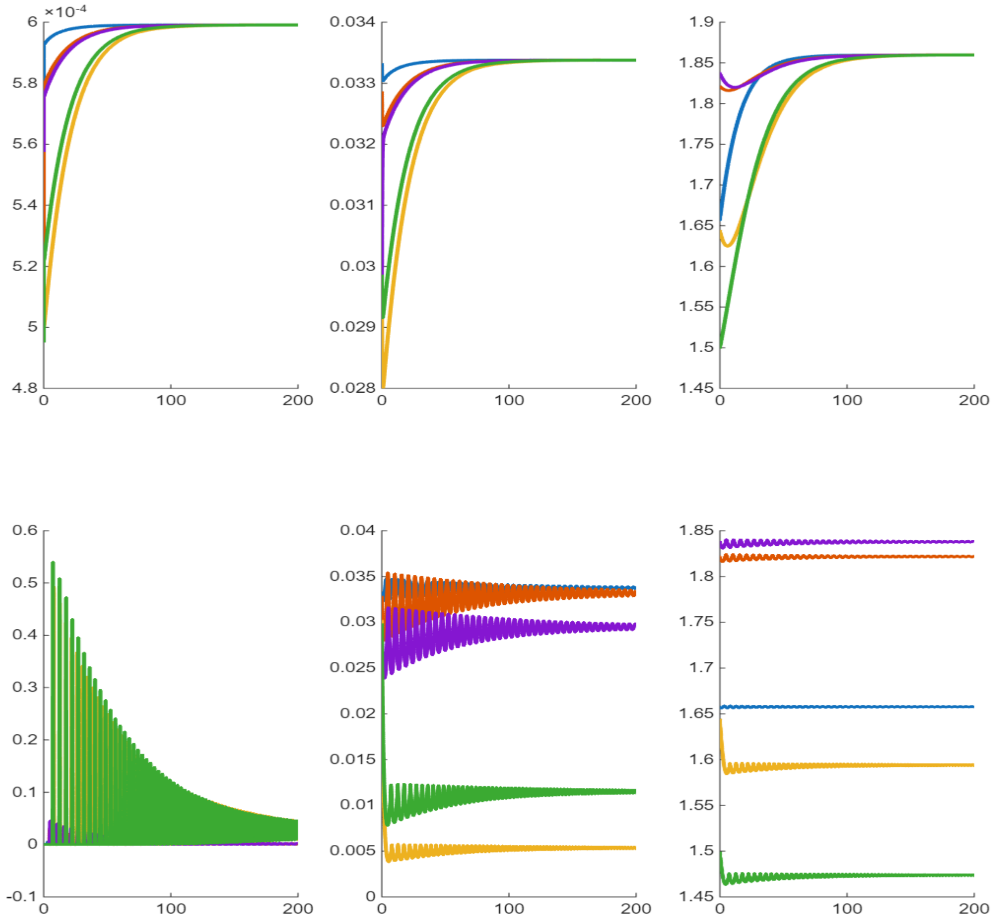

Figure R1: response of the smallest (left), middle (middle) and largest (right) sized organisms to 5 random different initial conditions for BORIS2 (top) and the same model without interference. It is seen that BORIS2 always converges on the same equilibrium solution whereas without interference the model converges on values that are different for each initial condition.

We agree that we should have given more information on how the interference function, *f*, performs in practice, including whether it acts differently for different size classes. The behaviour of the function is now shown (new Figure 2) and discussed in Section 2.4 (lines 234-241).

Personally, I think that it may be possible to achieve reasonable matches with the observations with more parsimonious parameterizations, if the scaling exponents for the other processes were allowed to vary. The scaling exponents for growth, respiration, and mortality are all the same and set to -0.1. It is not the most common practice amongst community/ecosystem models to set all of the biomass scaling exponents to be the same value. As the authors state in section 2.7, a more common scaling for growth and respiration would be around -0.2 or -0.25 (I think the theoretical prediction would be -0.25 but realistic values may vary). However, mortality is often assumed to have a different scaling than growth and respiration.

As described earlier, we have revised the model parameter values such that growth, respiration and mortality all now have scaling exponent -0.2, which is closer to the observations for the former two, as the referee indicates. Allowing the scaling exponent of mortality to vary would not provide an alternative solution to setting the scaling of biomass to assuming interference. First, as described above, if interference is removed, then the model becomes degenerate. Second, if we ignore the degeneracy arising from removing interference, and set a_i as constant to allow one of the other parameters to set the scaling of biomass then it is still not feasible for mortality to take on that role. Equation 11 demonstrates that for the scaling of B_i to be influenced significantly by m_i, then it is necessary to have $g_i >> m_i >> r_i$ such that m_i controls the scaling of the denominator in Equation 11 without being cancelled out by dominating the scaling of the numerator too. This would require either significantly reducing r_i, giving a substantially worse fit of total respiration to the POC flux, or increasing m_i, giving a much shorter lifetime (few years) of the largest organisms. Alternatively, $g_i >> r_i >> m_i$ could allow growth and respiration to set the biomass scaling with constant a_i (the biomass scaling would then be the difference of their two exponents), but the observed differences in scaling exponents for them (~0.05) are too small to be consistent with the observed ~0.25 scaling for biomass. However, the statement in the manuscript that all three rates have to share the same scaling exponent for a solution to exist is incorrect and has been removed. We now simply state that it is the simplest assumption - lines 187-188. It has also been corrected in Section 2.5 (lines 264-268)

Here, in this model, there is no representation of predators of these organisms (i.e., demersal fish) so I was a little surprised that the authors removed the quadratic loss term, and did not tune the mortality scaling to implicitly represent the role of predators within the ecosystem. In this case the emergent community structure then arises from the relationship between growth-respiration and mortality.

Can you describe a bit more what ends up being the closure term in the model, and if not – whether the lack of a closure term ends up constraining your parameter space so that bottom-up control can be the dominant control for the ecosystem?

The referee is right to point out that we don't have the usual quadratic closure for mortality i.e. mortality = d*B^2 gwwt/m2/d, where d is a parameter that scales with size. They imply that we could remove interference and instead use a quadratic mortality to get a well-behaved model. It is true that using a quadratic mortality would do this. However, we feel that there are good reasons to retain our current approach. Before explaining them we would like to clarify that the quadratic closure in the original BORIS model represented both natural mortality and predation. Natural predation has now been parameterised as a linear loss in BORIS2 because of incorrect lifespans arising from using a quadratic formulation – as described in lines 755-771. If a quadratic mortality was added to BORIS2 it would have to be in addition to the linear mortality and specifically to capture closure terms like predation from pelagic organisms, not natural mortality.

First, using such predation would require its own significant assumption. Adding a quadratic predation closure only gives a well-behaved model (i.e. one with unique solutions) if you include such a predation term for all size classes. We know of no observational data that we could use for a size dependent predation term. It might be possible to choose the scaling of predation on theoretical grounds which indicates that the scaling would need to be equal to the difference between the growth scaling (which is negative) and the biomass scaling (which is positive). Even using the conservative growth (-0.2) and biomass (+0.2) scaling exponents we use in the model (-0.2), this will give a predation scaling of -0.4, with a greater impact on smaller organisms (the opposite end of the size range to pelagic fish) and which is significantly ‘steeper’ than other ecological interactions we are aware of.

Second, while predation by pelagic fish may occur in more shallow environments like shelf seas, there is no strong evidence for it being a significant loss in deeper waters, which occupy a greater area. The model is deliberately simple, seeking to capture only first order processes. The dominant characteristic of benthic ecosystems is that they have a relatively flat trophic structure, with all organisms eating from the same resource to first order. This contrasts to the usual model for pelagic ecosystems where there is a ‘chain’ of one group/size eating another. Hence, we argue that the dominant influence in the benthic ecosystem is that of having neighbours competing for your food (rather than eating you) and this is what competition captures. To ensure this assumption is as clear as possible we have additionally added a statement at the start of the model description in Section 2.1 (lines 126-132).

Finally, for the benthos, the authors use the scaling exponent of the biomass size spectrum to constrain the model. I completely understand that these are very poorly observed systems and that available observational constraints are few and far in between. However, the danger in using the biomass size spectrum slope to validate the model is that very small variations in the size spectrum slope can have large implications for the total biomass. From a quick calculation, a 10% variation in the (normalized) biomass size spectrum slope (from -0.5 to -0.55) for a community that spans 10 orders of magnitude in size (e.g. 1 to 1e10 micrograms C) would result in a 3-fold difference in total community biomass. (This is using the fact that the normalized biomass size spectrum is integrable). Ecosystem modelers would certainly consider a 10% difference from an observed quantity to be an absolutely excellent match – but here the implications for total community biomass become quite large when the observed quantity used for model validation is a scaling exponent.

We agree with the referee that the total biomass may be sensitive to uncertainty in the biomass scaling exponent. However, we do not think the sensitivity is quite as strong as suggested. As already described, in revising the model parameter values we now assume a 0.2 scaling exponent for biomass instead of the 0.26 value indicated by fitting a power law to the observations. This is a 23% decrease in the scaling exponent. We have subsequently calculated the total biomass using the original power law fit to observations and the one forced to have an exponent of 0.2. The total biomass is reduced by a median of 55% across the sites, so effectively a factor of 2 difference. While still displaying sensitivity, this may be less pronounced than suggested by the referee because in addition to adjusting the slope the offset needs to be adjusted so that the fitted line still passes as closely as possible through the observations which are not evenly spread across the size range of organisms.

Nevertheless, it is clearly true that there is a significant sensitivity to the biomass scaling exponent. The referee questions the use of biomass as a constraint as a result. However, we feel it is justified given the alternatives. As described in the manuscript, observations of other potential constraints are just as uncertain, whether physiological rates (the variation in reported scaling exponent values, cited in the manuscript as between 0.11 and 0.25, is over a factor of two) or POC fluxes (which differ by an order of magnitude for CCZ). Returning to estimating total biomass, the model can never be more precise than our ability to measure total biomass observationally. For both pelagic and benthic biomass size spectra it may be very difficult to estimate true total biomass when very large / very rare individuals may be present. Obtaining asymptotic total biomass estimates may require field sampling unit sizes beyond the logistic limits of most field programmes (Ruhl et al., Integrating ocean observations across body-size classes to deliver benthic invertebrate abundance and distribution information. L&O Letters, 10.1002/lol2.10332, 2023). Even with this sensitivity we argue that BORIS2 is a useful tool for exploring relative changes in biomass, whether geographically or with time. If the primary interest for using the model is in carbon fluxes, then the first order issue is the uncertainty in the POC flux – but this is a problem shared with all benthic ecosystem models. At a second order level, once again the relative contributions of different size groups (here to energy use) are captured even if the absolute values may carry significant uncertainties.

What would enhance this manuscript would be a series of sensitivity studies showing focused (generally) on the range of parameter space for this model. I appreciated that the authors included section 2.7 but I found it difficult to follow without some examples in the manuscript.

This is a good point and an omission on our part. In Section 2.5, we have now presented (new Figure 5) and discussed (lines 423-441) an analysis showing how key metrics vary as each of the parameters is varied. We have additionally revised and expanded Section 2.7 to discuss these sensitivities more fully in the context of observational constraints, in response to the referee's final comment, discussed below.

Ideally, it would be great to see what the model results are when interference pre-factor were set to low values and the interference exponent was set to 0, combined with allowing beta of mortality to vary relative to the beta of growth and respiration, but I leave it up to the authors to decide what would be most appropriate.

We do not show the cases when the interference scaling exponent is set to zero and that for mortality allowed to vary independently for the reasoning given in our response to the referee's first and second points.

Lastly – it would be remis for me to write all this without noting that it is extremely difficult to model a system that is as poorly observed and understood as the benthos. All model representations of a new system must start somewhere and BORIS1/BORIS2 is notable as the first of its kind. I apologize for the somewhat rambling paragraphs above – but in my mind, all these model and parameter choices are all highly connected with each other.

There is absolutely no need for the referee to apologise. As the referee states, it is a challenging system to model giving the paucity of data and we are very grateful for their constructive review that encouraged us to us think more deeply about our approach and assumptions. We hope that we have managed to bring out the reasoning linking all our choices more clearly in responding to the referee's comments. We have also tried to acknowledge the important context highlighted by the referee. BORIS2 comes at an early stage in the development of benthic modelling and will be superseded. We are aware of this and try to assist this progression by indicating alternatives that people may want to consider as our knowledge of these systems improves. As part of this we have now added a short discussion (lines 678-690) of how bacteria may be treated differently in the model if a consensus (currently lacking) develops that this is necessary.

Minor comments

Lines 112-113, I think fg should be kg, right?

We think fg (=10^{-15} g) is correct when describing the smallest organisms.

Line 260, I found it confusing that the biomass scaling (alpha) was defined as a negative, resulting in values that are negative. I look into the benthos observations literature specifically and did not get the sense that this was common practice. If not common practice can you just use the raw values, allowing alpha to be positive?

We feel it would be odd to define the scaling of a_i as $-\alpha$ if that for the other rates was $+\beta$, especially if the two exponents share sign as they do. However, in the discussion of Figure 3 (lines 300-301, line 311 and Section 2.7 para 2) we have removed mention of α so that we can describe the scaling exponent of biomass as positive in line with convention.

Section 2.7, lines 385-384, 406-425. I overall like this discussion but found it hard to follow without some more concrete examples.

We have revised and expanded this Section 2.7 to give more examples, as requested, to illustrate the consequences of varying the parameter values within the uncertaintites.